ÉCOSCIENCE 12 (4): 455-465 (2005)

Nitrogen mineralization and decomposition in western boreal bog and fen peat[1]

Suzanne E. BAYLEY & Markus N. THORMANN[2], Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.
Anthony R. SZUMIGALSKI, Department of Plant Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada.

Abstract: The nitrogen (N) supply is limited in many peatlands, and the mineralization of organic matter represents a major source of N to plants. The goal of this paper is to establish the relationship between decomposition rates, mineralization rates, and the N concentration of peat along a peatland gradient in four peatlands in western, boreal Canada. The four peatlands differ physically, chemically, and floristically and include a bog, a poor fen, and two moderate-rich fens, one wooded and the other open. The fens are enriched by ground water inputs, which we hypothesized led to higher concentrations of N in peat, faster decomposition of litter, and higher N mineralization rates. Net N mineralization was virtually identical to net ammonification over a 2-y period, both measured using an *in situ* incubation technique. Net daily mineralization rates increased from the bog to the open, moderate-rich fen, with intermediate values in the poor fen and moderate-rich wooded fen. This increasing trend along the bog–open, moderate-rich fen peatland gradient was mirrored for mineralization rates on a temporal and spatial basis. Virtually no nitrification was detected in any of the sites. Estimated aboveground integrated ecosystem decomposition rates ranged from 17‰·y^{-1} in the bog to 31‰·y^{-1} in the wooded, moderate-rich fen. Decomposition rates were significantly correlated with the mean daily net N mineralization rate and with total N in the upper 20 cm of peat. The net mineralization rate also was positively correlated with the total N content of the peat in 1991. The total N content of the peat increased from 5.8 mg·g^{-1} in the bog to 11.5 mg·g^{-1} in the open, moderate-rich fen, with poor fen and moderate-rich wooded fen values intermediate. The total C content of the peat ranged from 370 to 400 mg·g^{-1} and was not significantly different among the four peatlands. TC:TN quotients for the peat cores were 68 in the bog and 36-38 in the fens, correlating negatively with net ammonification rates. Based on our data, the processes of mineralization of N and decomposition are tightly linked processes, both of which were higher in the fens than in the bog in our four western continental peatlands. Moreover, both processes are more affected by the quality of the organic matter, as indicated by the TC:TN quotients of the surface peat, than by surface water chemistry variables.
Keywords: bog, decomposition, fen, mineralization, nitrogen, peatlands.

Résumé : L'apport en azote est limité dans plusieurs tourbières. La minéralisation de la matière organique représente donc une source importante d'azote pour les plantes. Cet article vise à établir la relation entre le taux de décomposition, le taux de minéralisation et la concentration en azote de la tourbe le long d'un gradient de tourbières dans la zone boréale de l'Ouest du Canada. Quatre tourbières différant par leurs caractéristiques physiques, chimiques et floristiques ont été retenues, soit une tourbière ombrotrophe (bog), une tourbière minérotrophe (fen) pauvre et deux tourbières minérotrophes modérément riches, l'une boisée et l'autre ouverte. Les tourbières minérotrophes sont enrichies par des apports d'eau souterraine, ce qui leur permet, selon notre hypothèse, de bénéficier de plus grandes concentrations en azote dans la tourbe, d'une décomposition plus rapide de la litière et de taux plus élevés de minéralisation de l'azote. Nous avons utilisé une technique d'incubation *in situ* pour mesurer la minéralisation nette de l'azote et l'ammonification. La minéralisation nette de l'azote s'est avérée identique à l'ammonification nette après deux ans. Le taux de minéralisation journalier net s'est accru de la tourbière ombrotrophe à la tourbière minérotrophe modérément riche et ouverte. Nous avons observé des valeurs intermédiaires dans la tourbière minérotrophe pauvre et la tourbière minérotrophe modérément riche et boisée. Cette tendance à l'accroissement le long du gradient passant de la tourbière ombrotrophe à la tourbière minérotrophe modérément riche et ouverte se reflétait également au niveau des taux de minéralisation sur une base temporelle et spatiale. Aucune nitrification n'a été détectée dans les sites étudiés. Les taux estimés de décomposition de la biomasse aérienne de l'écosystème variaient de de 17 ‰·an^{-1} dans la tourbière ombrotrophe à 31 ‰·an^{-1} dans la tourbière minérotrophe modérément riche et boisée. Les taux de décomposition étaient corrélés de façon significative avec le taux journalier moyen de minéralisation nette de l'azote et avec le contenu total en azote des 20 cm supérieurs de tourbe. Le taux de minéralisation nette était également corrélé de façon positive avec le contenu total en azote de la tourbe en 1991. Le contenu total en azote de la tourbe est passé de 5,8 mg·g^{-1} dans la tourbière ombrotrophe à 11,5 mg·g^{-1} dans la tourbière minérotrophe modérément riche et ouverte. Des valeurs intermédiaires étaient observées dans les deux autres types de tourbière. Le contenu total en carbone de la tourbe variait de 370 à 400 mg·g^{-1} et n'était pas significativement différent entre les quatre tourbières. Le rapport carbone total - azote total des échantillons de tourbe était de 68 dans la tourbière ombrotrophe et de 36 à 38 dans les tourbières minérotrophes. Il était corrélé de façon négative avec le taux d'ammonification nette. Selon nos données, les processus de minéralisation de l'azote et de décomposition sont étroitement liés, les deux ayant été plus élevés dans les tourbières minérotrophes que dans la tourbière ombrotrophe. De plus, les deux processus sont plus affectés par la qualité de la matière organique, tel qu'indiqué par les rapports carbone total - azote total de la tourbe de surface, que par les variables chimiques de l'eau de surface.
Mots-clés : azote, décomposition, minéralisation, tourbière minérotrophe, tourbière ombrotrophe, tourbières.

Nomenclature: Anderson, 1990; Anderson, Crum & Buck, 1990; Moss, 1994.

[1]Rec. 2004-09-14; acc. 2005-02-14.
Associate Editor: John Khironomos.
[2]Author for correspondence. Present address: Northern Forestry Centre, 5320-122 St., Edmonton, Alberta T6H 3S5, Canada. e-mail: mthorman@nrcan.gc.ca

Introduction

Bogs are ombrotrophic peatlands that receive all of their nutrients from precipitation. In contrast, fens are minerotrophic peatlands that receive water and nutrients from subsurface and surface flow as well as precipitation. Because of the contribution of ground and surface water, it has been assumed that fens have more nutrients available for plant growth than bogs (Verhoeven, Maltby & Schmitz, 1990), although Vitt, Bayley, and Jin (1995) showed that nutrient concentrations in bog and fen waters are similarly low. Despite the low nutrient concentrations, flowing water could provide higher supplies of nutrients to fen vegetation.

With low levels of nutrients available to peatland vegetation from the water, internal cycling of nutrients is very important to plant growth (Bowden, 1987; Bridgham, Updegraff & Pastor, 1998). It is likely that mineralization processes are important in providing N for plant growth in bog (Urban & Eisenreich, 1988) and fen peatlands. Studies documenting the release of nutrients from decomposition and mineralization of the organic nutrients have been limited largely to fens, with few similar studies in bogs (Verhoeven, Maltby & Schmitz, 1990; Bridgham, Updegraff & Pastor, 1998; Scheffer, van Logtestijn & Verhoeven, 2001). Verhoeven, Kooijman, and Wirdum (1988), Verhoeven, Maltby, and Schmitz (1990), and Scheffer, van Logtestijn, and Verhoeven (2001) documented that mineralization of N is faster in *Sphagnum*-dominated European peatlands than in peatlands dominated by vascular plants and bryophytes other than *Sphagnum*. However, based on a literature review, Aerts, Verhoeven, and Whigham (1999) indicated that there are no clear differences in N mineralization rates in temperate fens and bogs in North America and Europe, suggesting that the dominant plant community has a strong influence on nutrient cycling dynamics in peatlands.

Mineralization and decomposition are closely linked processes and from a microbial perspective may be the same process. Decomposition generally refers to carbon and mass losses of organic matter, while mineralization generally refers to the transformations of N and P. While mineralization and decomposition may be part of the same process from an ecological perspective, different approaches are used to measure them. Decomposition is most often measured using litter bags (Bartsch & Moore, 1985; Ohlson, 1987; Verhoeven & Arts, 1992; Szumigalski & Bayley, 1996; Thormann & Bayley, 1997a; Scheffer, van Logtestijn & Verhoeven, 2001; Thormann, Bayley & Currah, 2001) or carbon fluxes (Bubier *et al.*, 1993; Roulet *et al.*, 1993; Yavitt, Wieder & Lang, 1993; Moore, 1994; Bellisario, Moore & Bubier, 1998; Chimner & Cooper, 2003). In contrast, mineralization is most often measured using an *in situ* incubation technique (Giblin *et al.*, 1991; Humphrey & Pluth, 1996; Mewhort, 2000). The close linkage between these processes has not been previously demonstrated in peatlands to our knowledge.

The goal of this paper is to establish the relationship between decomposition rates, N mineralization rates, and the N concentration of peat along a gradient of peatlands in western, boreal Canada. These peatlands included an ombrotrophic bog and three minerotrophic poor and moderate-rich fens. We examined the nutrients released during the processes of decomposition and N mineralization. We hypothesized that (1) fens have higher rates of N mineralization and decomposition than bogs (we examined one bog, one poor fen, and two moderate-rich fens), (2) plant litter quality limits rates of N mineralization and decomposition, and (3) decomposition and N mineralization are strongly linked processes in peatlands.

Methods

STUDY AREA AND SITE DESCRIPTIONS

The central Alberta study area is located 150 km north of Edmonton, Alberta, Canada, and is characterized by warm summers and cold, snowy winters. The mean annual temperature is 1.4 °C, and the total annual precipitation is approximately 490 mm (Environment Canada, 1998). The four sites represent the most common peatland types present in the area and included a bog (54° 41' N, 113° 28' W), a poor fen (PF, 54° 41' N, 113° 28' W), a wooded, moderate-rich fen (WMRF, 54° 28' N, 113° 17' W), and an open, moderate-rich fen (OMRF, 54° 28' N, 113° 17' W). Marshes, swamps, and extreme-rich fens are present in the region as well; however, they are less common (Vitt *et al.*, 1996) and were excluded from this study. Table I summarizes major characteristics of the four peatlands. More detailed descriptions of these sites are in Vitt, Bayley, and Jin (1995), Szumigalski and Bayley (1996; 1997), and Thormann and Bayley (1997a,b,c).

FIELD TECHNIQUES

MINERALIZATION

Mineralization experiments were carried out at two locations in each of the four peatlands from July to September 1990 and from May to July 1991. Four peat cores (15 cm in diameter and approximately 20 cm in length) were collected at each of the two locations in each peatland and cut longitudinally in half in the field. The first half was the "incubation core" and the second half was the "initial core" from which initial concentrations of NH_4^+-N and NO_3^--N were determined (see below). Since rates of nutrient mineralization vary with depth in response to changing environmental conditions, primarily oxygen availability, moisture content, pH, temperature, and litter/peat quality, we examined N mineralization rates in easily

TABLE I. Major physical and surface water chemistry characteristics (means and ranges) of the four peatlands in Alberta, Canada.

Peatland	Peat depth (m)	Bulk density ($g \cdot cm^{-1} \cdot m^{-2}$)	pH	NO_3^- ($\mu g \cdot L^{-1}$)	NH_4^+ ($\mu g \cdot L^{-1}$)	SRP ($\mu g \cdot L^{-1}$)
Bog	5	410	3.9 (3.4-4.2)	9 (3-24)	42 (12-108)	16 (1-63)
PF	4	580	4.9 (4.3-5.2)	11 (2-30)	21 (3-58)	72 (2-166)
WMRF	4.5	91	6.1 (5.7-6.6)	9 (2-25)	19 (2-34)	24 (3-147)
OMRF	1	92	5.8 (5.5-6.5)	14 (4-33)	26 (0-63)	10 (5-15)

Note: PF = Poor fen, WMRF = wooded moderate-rich fen, OMRF = open moderate-rich fen, and SRP = soluble reactive phosphorus. More detailed descriptions of these sites are provided in Vitt, Bayley, and Jin (1995), Szumigalski and Bayley (1996; 1997), and Thormann and Bayley (1997a,b,c).

106-03252/

demarcated sections of a continuous peat core. Both halves were sectioned into three layers distinguished by the degree of decomposition. The degree of decomposition was based only on visual and not physical or chemical characteristics. The top layer of each core was 0-4 cm or 0-3 cm and included all the live, green plant material. The 4-10 cm or 3-10 cm layer was lightly decomposed, light brown in colour, and with all the moss remains clearly identifiable. The third layer of the cores was the more decomposed, dark brown peat that retained its form and did not fall apart when the core was processed. Below that depth, the peat was completely humified, and we did not collect it. Due to differences in site characteristics, the deepest peat depth collected was the 10-15 cm zone in the two moderate-rich fens and the 10-20 cm zone in the bog and poor fen. All peat collected originated from the acrotelm (oxygenated peat horizon).

The peat core layers from the "incubation core" were placed in polyethylene bags (1.75 mm thickness) and replaced in the same hole from which they were removed initially. The bags were carefully squeezed to remove air and then sealed to ensure that the moisture content of each peat core layer was similar to the original, undisturbed state. This incubation bag technique is widely used despite having some limitations, *e.g.*, a constant moisture content and a different temperature regime from undisturbed peat, which may affect N dynamics inside the bags. Eight cores were collected in each site.

Decomposition

Decomposition rates of the dominant vegetation and a standard plant species were measured in the same peatlands from late September 1990 to early October 1991 (Szumigalski & Bayley, 1996). Hence, the decomposition and mineralization studies were initiated simultaneously. Briefly, in one set of measurements, aboveground plant material of the dominant plants was collected from the peatland sites. These were referred to as "native" species. Harvested samples consisted of the dominant moss species (terminal segments, 3 cm long) from each site and *Carex* species (senesced leaves, terminal segments, 5-7 cm long) from the fen sites. Entire leaves (senesced) and young branches (3-5 cm long) of the dominant shrub (*Betula pumila*) were also collected where present (Table II). One standard plant species, *Carex lasiocarpa* (senesced leaves, collected from a different, nearby fen), was used to compare decomposition rates in all four peatlands. This set of measurements is referred to as the "non-native" decomposition rate. Plant samples were dried at 60 °C for 24 h, and 0.3-2.7 g of the dried plant material was placed in pre-weighed nylon mesh bags (approximately 2.5 × 4.5 cm, 1-mm mesh gauge). Decomposition bags with the *Betula* samples contained approximately 0.55 g of leaves and 0.45 g of stems and branches for a total of 1.0 g per bag. Bags were placed horizontally just below the moss surface within each site. In October 1991, between five and 10 decomposition bags of each litter type were retrieved from each site. Forceps were used to remove coarse plant tissues, such as roots, growing into the litter bags; the bags were then carefully rinsed with distilled water to remove remaining "alien" matter, including fine plant and soil particles, dried at 60 °C for 24 h, and weighed to the nearest 0.1 g. The mass loss of each litter over the 1-y period was expressed as a percentage of the original mass.

TABLE II. Plant species in the four peatlands and their contribution (%) to the total aboveground NPP (net primary production, $g \cdot m^{-2} \cdot y^{-1}$). Only plant species that contributed > 5% to the total aboveground plant production are shown.

Plant species	Peatlands			
	Bog	PF	WMRF	OMRF *
DOMINANT SPECIES				
Sphagnum fuscum	155 (55%)			
Sphagnum teres and *Sphagnum angustifolium*		123 (40%)		
Carex spp.		37 (12%)	26 (7%)	111 (31%)
Betula pumila		83 (27%)	33 (9%)	
Tomenthypnum nitens			142 (40%)	
Hamatocaulis vernicosus				n.d. **
MINOR SPECIES				
Andromeda polifolia		19 (6%)	39 (11%)	28 (8%)
Rhododendron groenlandicum	60 (21%)			
Menyanthes trifoliata			29 (8%)	
Salix pedicellaris		27 (9%)	24 (7%)	
Larix laricina			38 (11%)	
Picea mariana	27 (10%)			
Aulacomnium palustre and *Sphagnum warnstorfii*				170 (48%)
Total site NPP	281	310	359	356

Note: NPP means from 1990 and 1991 (Szumigalski & Bayley, 1997); * based on Thormann (unpubl. data); ** based on visual observations only (Vitt, Bayley & Jin, 1995); site abbreviations as in Table I.

To compare decomposition rates of the entire peatland with the mineralization rate in that peatland, we developed an "aboveground ecosystem integrated decomposition rate" by prorating the decomposition by species as a function of the proportion each species contributes to the total annual aboveground plant production (Thormann, Szumigalski & Bayley, 1999; Hobbie & Gough, 2004). Briefly, the aboveground ecosystem integrated decomposition rate was obtained by measuring/calculating (1) the total aboveground net primary productivity of the dominant plant species in each peatland (in $g \cdot m^{-2} \cdot y^{-1}$), (2) the first year mass losses for each of the dominant species as described above (in %), and (3) the percent loss of each dominant species multiplied by the productivity of that species, yielding the mass lost due to decomposition (in g). Finally, the mass lost (in g) for all the dominant species was summed and divided by the total productivity of the dominant species for each peatland. Since we did not measure decomposition rates of all plant species in our peatlands, we used literature values to estimate decomposition rates of those species, or species with a similar growth habit if their decomposition rates had not been determined previously, whose contribution to the total aboveground plant production was > 5%. *Andromeda polifolia* was assumed to decompose similarly to *Vaccinium* spp., *Larix laricina* was assumed to decompose similarly to *Picea mariana*, *Menyanthes trifoliata* was assumed to decompose similarly to *Carex* spp., and *Sphagnum warnstorfii* was assumed to decompose similarly to *Sphagnum*

spp. from rich fens. By including these species and their respective above groundplant production, we accounted for > 86% of the total aboveground net primary production in each of the four sites (Table II). Hence, we refined the previously published aboveground integrated ecosystem decomposition rates (Thormann, Szumigalski & Bayley, 1999) by including these "minor" species before correlating them to our mineralization rates along the bog–fen peatland gradient. Although belowground plant production accounts for a significant proportion of the total net primary plant production in some peatlands (Backéus, 1990; Saarinen, 1996) and decomposition dynamics of belowground plant tissues vary significantly among plant litters (Thormann, Bayley & Currah, 2001), we did not measure these processes in this study.

LABORATORY TECHNIQUES

NH_4^+-N was extracted from the peat cores using 1 N KCl. NO_3^--N was extracted with distilled, deionized water. Water was used to extract NO_3^--N because the concentrations of NO_3^--N in peat were so low that the reagent-grade KCl added NO_3^- to the peat samples. The NH_4^+-N and NO_3^--N in the extracted peat were analyzed on a Technicon Autoanalyser (Technicon Instruments, Ardsley, New York, USA). Samples of initial and incubated peat at each depth were analyzed for total carbon (TC) and total nitrogen (TN) concentrations using a Control Equipment Corporation Model 440 Elemental Analyzer (Cazenovia, New York, USA).

The mineralization rate was calculated as the net ammonification rate plus the net nitrification rate. The net ammonification rate was the difference between the NH_4^+-N measured in the cores at the end of the incubation period and the NH_4^+-N extracted from the initial cores at the start of the incubation period. The nitrification rate was the difference between the NO_3^--N in the core at the end of the incubation period and the NO_3^--N extracted from the initial core. In most cases, the net ammonification rate was the same as the net mineralization rate, because there was almost no detectable NO_3^--N in the peat.

STATISTICAL ANALYSES

Chauvenet's criterion for the rejection of outliers (Kennedy & Neville, 1976) was applied to the raw data before statistical analyses were conducted (seven of 192 data points were eliminated). *T*-tests were used to compare the difference between years of the initial extractable N, net ammonification and mineralization rates, TN, and TC:TN quotients at each site, as well as to compare the difference between net ammonification rate and net mineralization rate in each year. One-way ANOVAs followed by Tukey Honestly Significant Difference tests were performed in SAS (SAS Institute Inc., 1988) to compare ammonification rates, initial extractable N concentrations in peat, and the litter quality of peat (TN and TC:TN) among depths within sites and among sites at each depth in 1990 and 1991 (generally $n = 8$ per site per depth per year for each of the three variables). Simple regressions of net ammonification rates ($n = 24$) against TN concentrations, TC:TN quotients, and aboveground integrated ecosystem decomposition rates (n = 10-30, depending on the number of dominant plant species in each peatland) were then conducted for the 1991 data only, since the 1990 ammonification data preceded the 1-y decomposition period and should not be regressed against each other. These regressions did not include ammonification rates from the 0-4 cm core segments, because that layer consists of living plant tissues that mineralize differently due to higher nutrient concentrations compared to the dead plant tissues at greater peat depths (bog, PF: 4-20 cm; WMRF, OMRF: 4-15 cm).

Results

NET AMMONIFICATION

Conversion of organic N to NH_3 was more important than nitrification in providing an inorganic source of N to plants in these peatlands. The net ammonification rate and the net mineralization rate were virtually identical in 1990 and 1991 and increased along the bog–fen peatland gradient (ammonification rates shown only; Figures 1a,b). Net nitrification rates were essentially zero in all four peatlands (data not shown). Analysis of the mineralization rate at the various depths in the peat profile also showed that little NO_3^--N was produced and that the net mineralization rate was almost identical to the ammonification rate at each depth (data not shown). Ammonification rates were highest in the surface 0-4 cm and decreased with depth. The OMRF had the highest ammonification rate in the surface layer in both years. The bog had substantially lower ammonification rates than any other peatland at all depths (Table III).

DECOMPOSITION OF THE DOMINANT VEGETATION

The aboveground integrated ecosystem decomposition rate increased along the bog–rich fen peatland gradient and was 17%·y^{-1} in the bog and 31%·y^{-1} in the WMRF. Decomposition rates in the PF and OMRF were intermediate and similar to each other (27 and 26%·y^{-1}, respectively). These rates were positively correlated with the mean daily net ammonification rates in the four peatlands ($r^2 = 0.66$; Figure 2). Decomposition rates of *C. lasiocarpa* (used in all sites to provide a cross-site comparison) ranged from 33% (OMRF) to 45% (bog, PF) mass loss in the first year (Table IV). Mass losses of the mixture of native dominant *Carex* spp. were higher than the cross-site standard *Carex* litter (50-58% after the first year; significant in the WMRF, $P = 0.00027$, and OMRF, $P = 0.00001$; Table IV).

INITIAL EXTRACTABLE N IN PEAT

Initial extractable N (NH_4^+ and NO_3^-) was measured in the three layers of the mineralization cores. Extractable NH_4^+-N was approximately 100x higher in concentration than was extractable NO_3^--N. Initial extractable NO_3^--N was very low at all depths in all the peatlands measured, ranging from 1.1 to 3.5 mg N·kg dry peat^{-1} (data not shown). In 1990, initial extractable N (measured as mg NH_4^+-N·kg dry peat^{-1}) in the total core (0-20 cm) was lowest in the bog (178 mg N·kg dry peat^{-1}), higher in the PF and WMRF, and highest in the OMRF (604 mg N·kg dry peat^{-1}) (bog, PF: 20-cm core; WMRF, OMRF: 15-cm core; Table V). The values for each site were generally significantly higher than those obtained in 1991, but the pattern across the bog–fen peatland gradient was similar ($P < 0.05$). The amount of NH_4^+-N in peat also varied with depth. In the surface layer, the OMRF consistently had significantly higher NH_4^+-N

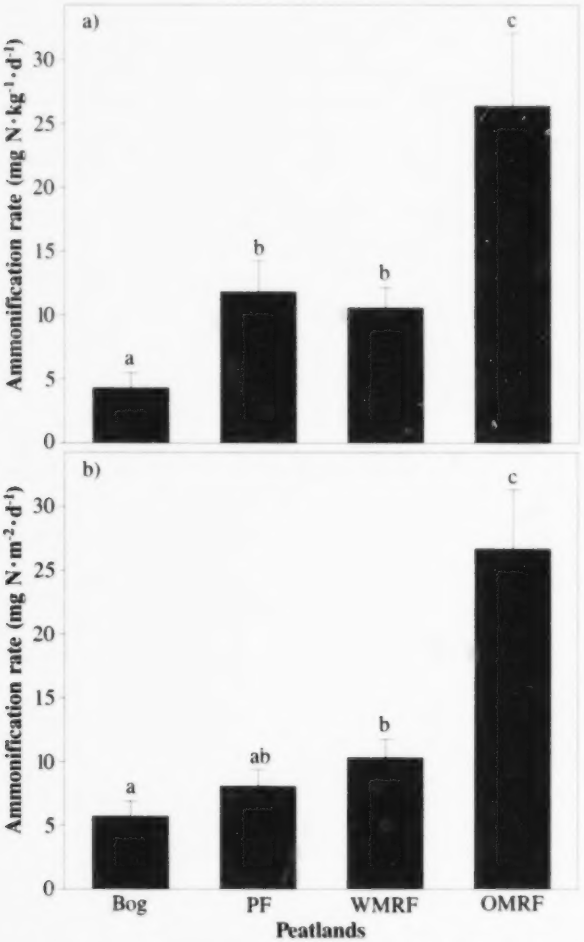

FIGURE 1. a) Net ammonification rates (± SE) in the entire peat core from the bog and fen peatlands on a volume basis in 1991. b) Net ammonification rates (± SE) in the entire peat core in the bog and fen peatlands on an aerial basis in 1991. PF = poor fen, WMRF = wooded, moderate-rich fen, OMRF = open, moderate-rich fen. Different letters indicate significant differences ($P < 0.05$) among peatlands for each panel. Bog and PF, 20-cm cores; WMRF and OMRF, 15-cm cores.

TABLE III. Net ammonification rate (mg N·kg dry peat^{-1}·d^{-1}, means ± SE) in peat cores from four peatlands in Alberta, Canada. $n = 8$ per treatment.

Time	Peatland	Depth of layer (cm)		
		0-4	4-10	10-20
SUMMER 1990				
	Bog	2.6 ± 0.4^{a1}	0.5 ± 0.2^{b1}	0.3 ± 0.2^{b1}
	PF	8.1 ± 3.0^{a2}	4.4 ± 1.2^{b2}	0.9 ± 0.4^{c1}
	WMRF *	2.7 ± 0.3^{a1}	1.5 ± 0.3^{a1}	-0.6 ± 0.8^{b1}
	OMRF *	10.1 ± 1.0^{a2}	4.1 ± 0.7^{b2}	0.6 ± 0.4^{c1}
SPRING 1991				
	Bog	2.4 ± 0.7^{a1}	1.0 ± 0.4^{b1}	0.8 ± 0.1^{b1}
	PF	5.5 ± 1.2^{a2}	3.0 ± 0.7^{a2}	2.9 ± 0.9^{a1}
	WMRF *	4.5 ± 0.7^{a2}	3.7 ± 0.9^{a2}	2.4 ± 0.3^{a1}
	OMRF *	19.8 ± 3.3^{a3}	5.5 ± 2.3^{b2}	2.2 ± 0.6^{b1}

Note: Peatland abbreviations as in Table I; net mineralization rates (mg N·kg dry peat^{-1}·d^{-1}) were identical to net ammonification rates; * = 10-15 cm only (see Methods); different italic letters indicate significant differences among depths within sites, and different italic numbers indicate significant differences among sites for each depth for each year.

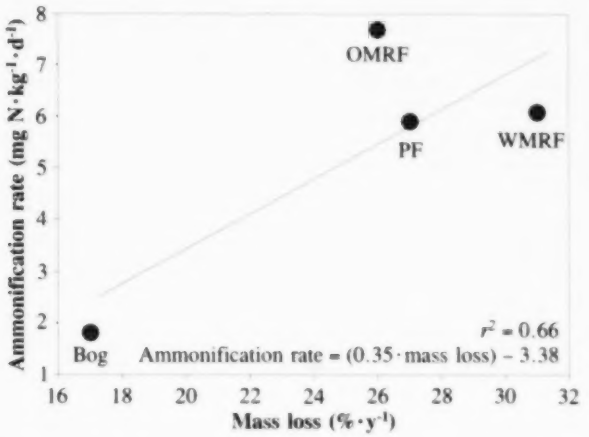

FIGURE 2. Regression of the net N ammonification rate *versus* the aboveground ecosystem integrated decomposition rate in the 4-20 (bog, PF) and 4-15 cm (WMRF, OMRF) segments of peat cores in 1991. Each ammonification data point is the mean of 16 samples and each decomposition data point is the mean of 10-30 samples depending upon the number of dominant plant species in each peatland. Site abbreviations as in Figure 1.

concentrations than any other site ($P = 0.0001$), while those in the bog were the lowest (statistically significant only in 1990; $P = 0.0001$). In the deepest layer measured, the WMRF had the significantly highest and the bog the significantly lowest concentration of NH_4^+-N ($P = 0.0001$; Table V).

TOTAL N AND TOTAL C CONTENT AND TC:TN QUOTIENTS OF PEAT

The TN content of the surface layer was generally lowest in the bog and highest in the OMRF (Table VI). In 1990, the TN content of the bog peat was significantly lower than in the fen sites ($P = 0.00001$), but there was no significant difference among the three fen sites ($P > 0.05$). In 1991, the OMRF was significantly higher than the other peatlands ($P = 0.00001$). The TN content in the bog was significantly higher in the upper (0-4 cm) than in the lower (4-10 and 10-20 cm) peat depths ($P = 0.035$ and $P = 0.002$ in 1990 and 1991, respectively). In the WMRF, the deepest peat layer had a higher TN concentration; however, this was significant only in 1991 ($P = 0.007$). TN content at all depths in the OMRF was not significantly different ($P > 0.05$; Table VI). There was a strong relationship between the amount of TN initially present in the peat and the amount of N mineralized ($r^2 = 0.84$; Figure 3a). There was also a good positive relationship between the net ammonification and integrated ecosystem decomposition rates (Figure 2) and a weaker, but significant, positive relationship between decomposition rates and TN of the litter ($r^2 = 0.31$; Figure 3c).

The TC content of the initial cores calculated on the basis of the entire core ranged from 367 to 404 mg·g^{-1} in the bog and fens. There was generally no difference in TC content of peat in the four peatlands or at any of the three depths measured (data not shown), except in the deepest layer of the OMRF, which was significantly higher in TC content than the other layers ($P = 0.002$). In 1990, the TC:TN quotient for the entire core was 68 in the bog, 37 in the PF, 35 in the OMRF, and 38 in the WMRF. The bog generally had

TABLE IV. Mass losses of plant species per year (mean % ± SE). n = 5-10 per plant species. Only plant species that contribute > 5% to the total aboveground plant production are shown.

Plant litters	Peatlands			
	Bog	PF	WMRF	OMRF
DOMINANT SPECIES *				
Sphagnum fuscum	14 ± 1.4			
Sphagnum teres and *Sphagnum angustifolium*		16 ± 0.6		
Carex spp.		50 ± 1.7^{a}	58 ± 2.1^{b}	50 ± 1.8^{a}
Betula pumila		36 ± 1.0^{a}	37 ± 1.3^{a}	
Tomenthypnum nitens			22 ± 3.8	
Hamatocaulis vernicosus				10 ± 1.4
MINOR SPECIES **				
Andromeda polifolia		36	36	36
Rhododendron groenlandicum	25			
Menyanthes trifoliata			58	
Salix pedicellaris		28	43	
Larix laricina			29	
Picea mariana	29			
Aulacomnium palustre and *Sphagnum warnstorfii*				16
CROSS-SITE STANDARD LITTER *				
Carex lasiocarpa	45 ± 4.1^{a}	45 ± 5.2^{a}	42 ± 1.9^{a}	33 ± 1.4^{b}
INTEGRATED ECOSYSTEM DECOMPOSITION RATE	17	27	31	26

Note: Site abbreviations as in Table I; data previously published in * Szumigalski and Bayley (1996); ** mass losses were estimated from the literature; decomposition rate of *A. polifolia* was assumed to be similar to *Vaccinium* spp., decomposition rate of *L. laricina* was assumed to be similar to *P. mariana*, decomposition rate of *M. trifoliata* was assumed to be similar to *Carex* spp., and the decomposition rate of *S. warnstorfii* was assumed to be similar to *Sphagnum* spp. in rich fens; italic letters indicate significant differences in mass losses of the same litter type among sites.

TABLE V. Initial extractable nitrogen (mg N·kg dry peat^{-1}, means ± SE) in peat cores from four peatlands in Alberta, Canada. n = 8 per depth per site and n = 24 per core.

	Depth of layer (cm)			
Peatland	0-4	4-10	10-20	Whole core
SUMMER 1990				
Bog	86 ± 6^{a1}	26 ± 2^{b1}	66 ± 4^{ab1}	178 ± 12^{1}
PF	139 ± 15^{a2}	159 ± 16^{a2}	170 ± 14^{a2}	468 ± 31^{3}
WMRF *	105 ± 15^{a2}	100 ± 13^{a3}	287 ± 30^{b3}	492 ± 44^{3}
OMRF *	312 ± 45^{a3}	192 ± 41^{b2}	100 ± 9^{c4}	604 ± 79^{3}
SPRING 1991				
Bog	51 ± 7^{a1}	28 ± 6^{b1}	26 ± 4^{b1}	105 ± 16^{2}
PF	63 ± 9^{a1}	70 ± 15^{a2}	68 ± 8^{a2}	201 ± 21^{1}
WMRF *	89 ± 9^{a1}	125 ± 18^{a3}	132 ± 14^{a3}	346 ± 20^{4}
OMRF *	318 ± 47^{a2}	140 ± 17^{b3}	71 ± 9^{c2}	529 ± 48^{3}

Note: Peatland abbreviations as in Table I; * = 10-15 cm only (see Methods); italic letters and numbers defined as in Table III. Whole core data were analyzed separately among sites and between years.

a significantly higher TC:TN quotient at any depth than did the fens (P = 0.00055 or less) due to the lower concentration of TN in the peat (Table VI). In 1991, the OMRF had a significantly lower TC:TN quotient than the other peatlands (P = 0.0001) due to substantially higher TN peat concentrations (Table VI). In 1991, the bog had a significantly lower TC:TN quotient in the top layer compared to deeper layers in the peat profile (bog: P = 0.0021). There was a strongly negative relationship between the net ammonification rate and the TC:TN quotient in these Alberta peatlands (r^2 = 0.92; Figure 3b). Similarly, there was a significant negative relationship between the ecosystem decomposition rate and the TC:TN quotient of the peat (r^2 = 0.48; Figure 3d).

Discussion

N MINERALIZATION RATES IN THE BOG AND FENS PEATS

Mean daily net N mineralization rates in the upper 10 cm in the bog were equivalent to those measured in the Netherlands (2.3 and 3.4 *versus* 4.4 mg N·kg^{-1}·d^{-1}), while net mineralization rates in the Alberta fens were 1.6-5x higher than the Dutch rates (Verhoeven, Kooijman & Wirdum, 1988; Verhoeven, Maltby & Schmitz, 1990). We found that the bog had the lowest rate, the WMRF and PF had intermediate rates, and the OMRF had the highest rate of mineralization, supporting hypothesis 1, which stated that fens have higher net mineralization rates than bogs. This conclusion has to be taken with caution, however, since we had no true replication of sites. Our data are in contrast to Verhoeven, Maltby, and Schmitz's (1990) findings that bogs had higher rates of mineralization than fens and Scheffer, van Logtestijn, and Verhoeven's (2001) findings where *Sphagnum*-dominated fens had higher net mineralization rates than *Carex*-dominated fens. Both of those studies were conducted in the Netherlands. Another study by Verhoeven *et al.* (1994) compared Dutch and American (Maryland) bogs and fens and had different results; the herb-dominated bogs in both countries had low N mineralization rates (< 0.5 mg N·kg^{-1}·d^{-1}), while the fens had higher rates. A similar trend of increasing N mineralization rates has been reported by Updegraff *et al.* (1995) and Bridgham, Updegraff, and Pastor (1998) along an ombrotrophic-minerotrophic peatland gradient in Minnesota. Although individual studies may show clear trends of increasing or decreasing N mineralization rates among different peatlands, Aerts, Verhoeven, and Whigham (1999) summarized N mineralization rates from temperate fens and bogs in the Netherlands, Poland, and the USA (Maryland) and found no clear differences among them. They attributed this in part to the influence of different plant communities in different peatlands.

Rosswall and Granhall (1980) stated that 0.44-0.57 mg N·kg^{-1}·d^{-1} was mineralized in a subarctic ombrotrophic peatland, all of which was remineralized to NH_4^+-N. They did not detect any nitrification or NO_3^--N present in water or peat. We also found that essentially all of the mineralization was as NH_4^+-N and little NO_3^--N was detected in the peat. Williams and Wheatley (1988) concluded that nitrification is unlikely in sites with poor aeration, high acidity, and a restricted supply of ammonium. In contrast, Bridgham, Updegraff, and Pastor (1998) detected nitrification in peatlands along an ombrotrophic-minerotrophic gradient in Minnesota. Their peatlands had a pH range from 3.76 to 5.95, which is similar to our pH range (3.9-6.1; Table I). They showed that nitrification rates lagged in their more acidic peatlands, suggesting that acidity inhibits nitrification to some degree.

TABLE VI. Total nitrogen (TN) content ($mg \cdot g^{-1}$) and TC:TN quotients (means ± SE) of peat in three depth layers (cm) from four peatlands in Alberta, Canada. $n = 8$ per treatment.

Peatland	TN			TC:TN		
	0-4	4-10	10-20	0-4	4-10	10-20
SUMMER 1990						
Bog	7.1 ± 0.6^{a1}	5.1 ± 0.3^{b1}	5.4 ± 0.6^{b1}	54 ± 4^{a1}	79 ± 6^{b1}	71 ± 6^{b1}
PF	11.3 ± 0.4^{a2}	9.3 ± 0.6^{b2}	13.0 ± 1.2^{a2}	35 ± 1^{a2}	42 ± 2^{b2}	33 ± 3^{a2}
WMRF *	9.3 ± 0.5^{a2}	9.4 ± 0.7^{a2}	11.5 ± 0.8^{a2}	42 ± 2^{a3}	41 ± 3^{a2}	31 ± 2^{b2}
OMRF *	11.1 ± 0.6^{a2}	nd	12.0 ± 0.5^{a2}	35 ± 2^{a2}	nd	35 ± 2^{a2}
SPRING 1991						
Bog	8.1 ± 0.3^{a1}	5.5 ± 0.5^{b1}	6.8 ± 0.5^{b1}	47 ± 2^{a1}	63 ± 5^{b1}	61 ± 4^{b1}
PF	9.5 ± 0.6^{a1}	8.0 ± 0.4^{a2}	8.3 ± 0.7^{a2}	41 ± 2^{a2}	48 ± 2^{a2}	41 ± 6^{a2}
WMRF *	7.6 ± 0.5^{a1}	9.1 ± 1.0^{b2}	11.8 ± 0.9^{b3}	47 ± 3^{a1}	47 ± 6^{a2}	32 ± 3^{b3}
OMRF *	12.9 ± 0.5^{a2}	11.7 ± 0.4^{a3}	12.3 ± 0.7^{a3}	29 ± 1^{a3}	31 ± 1^{a3}	33 ± 2^{a3}

Note: Site abbreviations as in Table I; TC = total carbon (data did not differ among depths within sites, not shown); nd = no data; * = 10-15 cm only (see Methods); italic letters and numbers defined as in Table III.

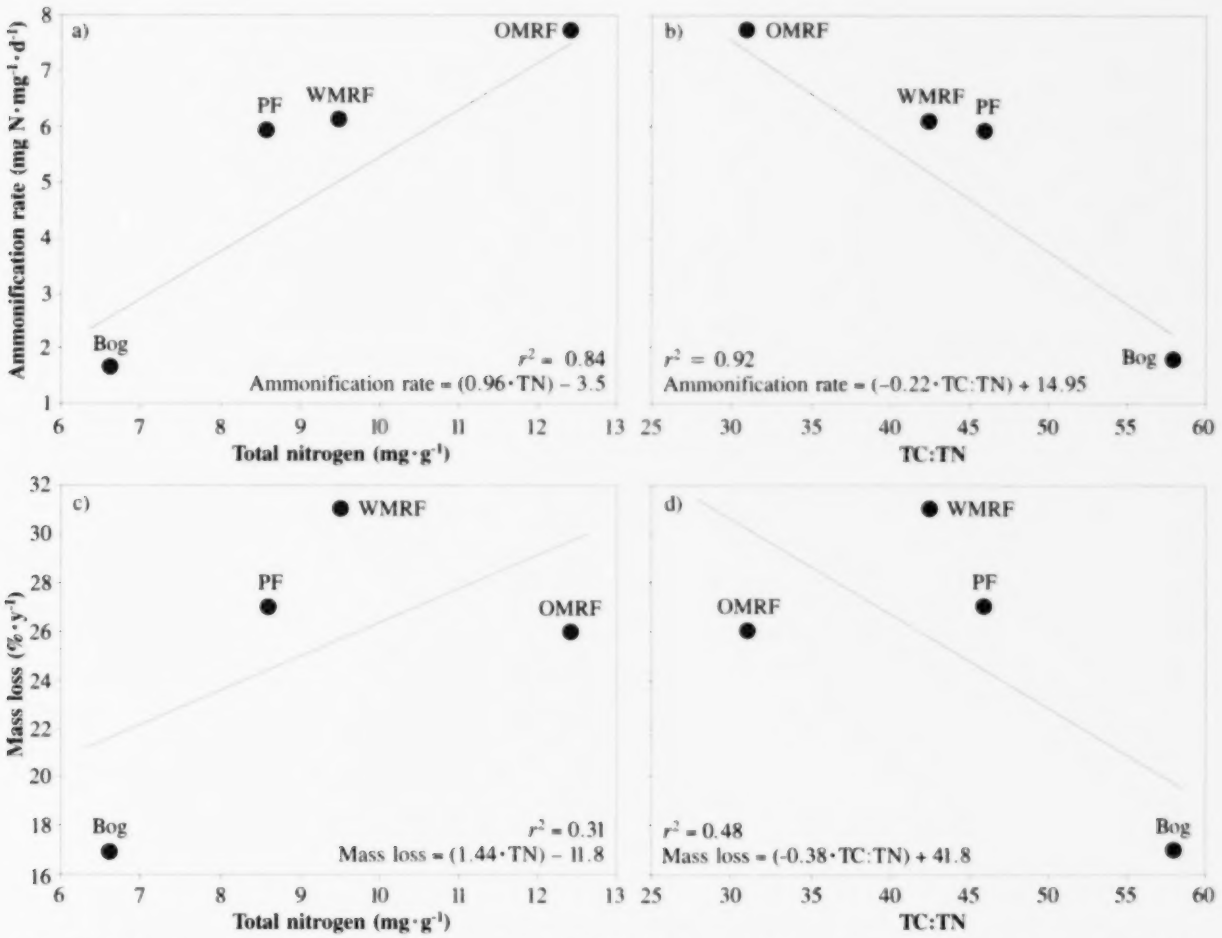

FIGURE 3. a) Regression of mean total nitrogen in peat cores from the bog and fens in central Alberta *versus* the net N ammonification rate in the same peat profiles. Each data point is the mean of 24 samples. b) Regression of the mean TC:TN quotient in peat cores from the bog and fens *versus* the net N ammonification rate in the same peat profiles. Each data point is the mean of 24 samples. c) Regression of mean total nitrogen in peat cores from bog and fen peatlands *versus* the aboveground integrated ecosystem decomposition rate from the same peatlands. Each decomposition data point is the mean of 10-30 samples depending on the number of dominant plant species in each peatland. d) Regression of the mean TC:TN quotient in peat cores from the bog and fens *versus* the aboveground integrated ecosystem decomposition rate from the same peatlands. Each decomposition data point is the mean of 10-30 samples depending on the number of dominant plant species in each peatland. Site abbreviations as in Figure 1. Bog and PF, 4- to 20-cm core segments; WMRF and OMRF, 4- to 15-cm core segments. Only 1991 data were used in these regressions.

One question raised by our data is, why was there no evidence of nitrification in our fens? Particularly in the moderate-rich fens, we expected to detect NO_3^--N produced during the incubation period, since the higher pH (5.8-6.1; Table I) should not inhibit microbial activity. There are several potential explanations. First, at low levels of aeration, nitrifying bacteria may not be able to compete with methanotrophic bacteria, which are known to inhibit nitrification (Megraw & Knowles, 1987). Thus, despite the higher pH in the moderate-rich fens, the lack of nitrate could be due to the presence of methanotrophs, which probably use the methane that is abundantly produced in these sites (Mewhort, 2000; S. E. Bayley, unpubl. data). Second, we did observe low levels of NO_3^--N in the surface water of the fens (Vitt, Bayley & Jin, 1995), but this could also come from ground water input. Third, any NO_3^--N formed by nitrification following the initiation of the mineralization study could have been denitrified during the incubation period as redox potentials may have decreased in the polyethylene bags (not measured in this study). Fourth, nitrification could have been offset by nitrate reduction as well as by nitrate uptake.

Surface ammonification rates (0-4 cm) were higher than ammonification rates at greater depths (> 4 cm; Table III). Williams and Wheatley (1988) found that mineralization rates in the top 10 cm were higher than rates in the 20-50 cm depth. They also found that in sites where the water table was lowered by drainage, the numbers of ammonifying bacteria increased and the mineralization of N increased. This is similar to the findings in forest systems, where mineralization was higher in the surface organic layers than in the deeper layers (Pastor *et al.*, 1984). Humphrey and Pluth (1996) determined that N mineralization rates were unaffected by drainage, (*i.e.*, greater aeration) in Alberta fens with a pH below 6.6 and that drainage only increased N mineralization rates above pH 7.2. However, they cautioned that the altered peat bulk density due to drainage may have obscured the influence of pH. Bulk density was also identified as a significant variable influencing N mineralization rates in Minnesota peatlands by Bridgham, Updegraff, and Pastor (1998).

RELATIONSHIP BETWEEN DECOMPOSITION AND MINERALIZATION RATES

Mass losses of bryophytes ranged from 10 to 22%·y^{-1} (*Sphagnum* species, *Tomenthypnum nitens*, and *Hamatocaulis vernicosus*) and were substantially lower than those of vascular plant species in the bog and fens (36-58%·y^{-1}; *Carex* spp., *B. pumila*; Table IV). The cross-site standard plant species, *C. lasiocarpa*, decomposed similarly well in the bog, PF, and WMRF, but significantly more slowly in the OMRF ($P = 0.003$; Table IV). Comparisons of our mass losses to those from other studies are provided in Szumigalski and Bayley (1996).

The aboveground integrated ecosystem decomposition rate indicates a gradient in decomposition rates, with the bog having the lowest and the WMRF having the highest decomposition rate (Table IV). These data support hypothesis 1, which stated that decomposition rates are greater in fens than bogs, likely due to litter quality characteristics of the indigenous plants in bogs and fens. In order to properly explore the relationship between decomposition and mineralization rates in our four peatlands, it was necessary to estimate decomposition rates, since it is meaningless to correlate mineralization rates from cores consisting of heterogeneous plant materials (peat) to decomposition rates of individual plant species. Our estimate of the aboveground integrated ecosystem decomposition rate is a blend of the decomposition rates of individual plant species weighted by their relative dominance from a plant community perspective, *i.e.*, their contribution to the total aboveground net primary production (Table II). Hence, it is not simply a mean of the decomposition rates of the individual plant species examined in each of the four peatlands, but takes into consideration the dominance of each of the plant species examined as well. The actual aboveground integrated ecosystem decomposition rates for these four sites may be different from our estimated ones: errors may have been introduced in the course of (1) assessing the aboveground plant production of individual species (all major species were measured), (2) assessing their decomposition rates (most species were measured), (3) using literature-derived decomposition rates for a few unmeasured plant species, and (4) estimating decomposition rates of selected species that had never been measured. However, it does not seem likely that the actual decomposition rates of these four peatlands differ drastically from our estimated aboveground integrated ecosystem decomposition rates.

Breakdown of organic matter releases the organically bound N; consequently, we expected microbial decomposition and N mineralization to be correlated, providing that the N released is not immediately immobilized by microbes. We found a positive relationship between the aboveground integrated ecosystem decomposition rates and ammonification rates ($r^2 = 0.92$; Figure 2). This is in contrast to Verhoeven, Maltby, and Schmitz (1990), who found an inverse relationship between mineralization and decomposition rates. They found the highest decomposition rates associated with lower mineralization rates in fens, while the *Sphagnum*-dominated bogs had low decomposition but higher mineralization rates. They hypothesized that the low decomposition rate in the bogs was due to the inhibition of microbes and that these sites had high N mineralization rates because there was no immobilization of N, due to the low microbial activity. Our findings of a positive relationship between decomposition and net mineralization are what we would expect, because fungi and bacteria degrade organic matter, releasing N in the process. The released N appears not to be immobilized by fungi or bacteria in either the bog or the fens; however, our data cannot support or refute the apparent lack of microbial N immobilization in our peatlands. Although it is generally stated (Parnas, 1975) that net N immobilization occurs at TC:TN quotients above 15-20, this does not appear valid for bogs (Damman, 1988; Verhoeven, Maltby & Schmitz, 1990). These studies (especially Damman, 1988) suggest that there is net N mineralization in bogs (at low pH and high TC:TN quotients) because microbial growth is limited and N does not limit decay. In our study, we have net N mineralization in the bog as well as the fens and the TC:TN quotients generally are > 35.

Net mineralization rates in the peat profile were correlated with decomposition rates of native dominant plant species; however, the litter decomposition rate of the transplanted *Carex* was apparently unaffected by differences in N availability, as estimated by net N mineralization. The decomposition of the transplanted *Carex* was probably related to the chemistry of the *Carex* plants, and the N mineralized in the peat profile did not affect its decomposition. This suggests that the net N mineralization rate does not affect the initial decomposition rate, similar to the findings of McClaugherty *et al.* (1985) in northern hardwood forest litter. We observed a positive correlation between the net N mineralization rate and the decomposition of native plant species on an integrated aboveground ecosystem basis (Figure 2). However, we do not know how decomposition influences the mineralization rate or *vice versa*. Specifically, we do not know which organic constituents were actually accessed and how rapidly they were subsequently metabolized by microbes. McClaugherty *et al.* (1985) found higher mineralization rates in forest stands where the forest litters had lost more of their acid-insoluble material, suggesting that N mineralization was related to the breakdown of recalcitrant material in the forest floor. Farrish and Grigal (1988) detected more lignin in their fen peat than in their bog peat due to the preferential degradation of the more easily metabolizable organics relative to complex compounds.

We obtained an inverse relationship between decomposition rates and TC:TN quotients of the different peatland litters (Figure 3d), indicating that litters with higher TC:TN quotients and hence lower TN concentrations decompose more slowly than those with lower TC:TN quotients and hence higher TN concentrations (Figure 3c). If the TC:TN quotient is used as an estimate of litter quality, as it has been in some forest litter studies (Berg & Staaf, 1981; Vitousek *et al.*, 1982; Pastor *et al.*, 1984), then bog surficial peat with a mean TC:TN quotient of 51 is of lower quality than surficial peat in the OMRF with a mean TC:TN quotient of 32, due to lower TN in the peat in the former (Table VI). Rates of net N mineralization (or ammonification) were highly negatively correlated with the TC:TN quotients of the 4-20 cm segment of the peat cores (Figure 3b), so there is likely a relationship between the quality of the organic constituents and the net mineralization rate. In conjunction with the negative correlation between litter quality and aboveground integrated ecosystem decomposition rates (Figure 3d), we accept hypothesis 2, which stated that litter quality limits N mineralization and decomposition rates.

Chemical properties of peat and the relationship to mineralization rates

The extractable N content of peat in the four Alberta peatlands was generally low, although it was significantly higher in the OMRF than in the bog at any depth ($P = 0.0001$; Table V). The generally substantially lower initial extractable N in 1990 compared to 1991 may be due to the different incubation periods (summer *versus* spring, respectively) and the resultant differences in environmental conditions such as temperature, moisture content, microbial community composition and activity, and phenology of the plant community. In contrast to our results, Waughman and Bellamy (1980) in their analysis of German mires did not detect any gradient in TN content in either vegetation or peat. The TN in peat in their bogs and fens ranged from 11 to 18 $mg \cdot g^{-1}$, while the N in vegetation ranged from 16 to 18 $mg \cdot g^{-1}$, all of which were higher than our values (Table VI). Their sites in southern Germany had received high anthropogenic N deposition for many years, which may have influenced their results. In general, the gradient data from German mires have higher TN and lower NH_4^+-N in the peat than do our Alberta peatlands (Waughman & Bellamy, 1980). While this could mean that the German peatlands are more N limited, it could also be an indication that anthropogenic sources of N rather than mineralization are supplying more of the required N. If more of the nutrients are supplied by the atmosphere, it is possible that the lower NH_4^+-N, which we observed, is due to lowered mineralization of organic N. The NH_4^+-N concentrations in peat from the four Alberta peatlands did show differences across the peatland gradient, although that was mainly due to higher values in the OMRF (Table V). There was a poor relationship between extractable N and net mineralization rate across the peatland gradient. Waughman and Bellamy (1980) observed a gradient in NH_4^+-N in peat, with the highest values in the bog and lower values in the fen sites. This could be due to reduced mineralization in the fen sites, where plants receive both N-enriched ground water and high N from anthropogenic deposition and thus do not require the N from mineralization. This might also explain why Verhoeven, Maltby, and Schmitz (1990) measured lower mineralization rates in fens than in bogs in the Netherlands, which is also in an area of high N deposition.

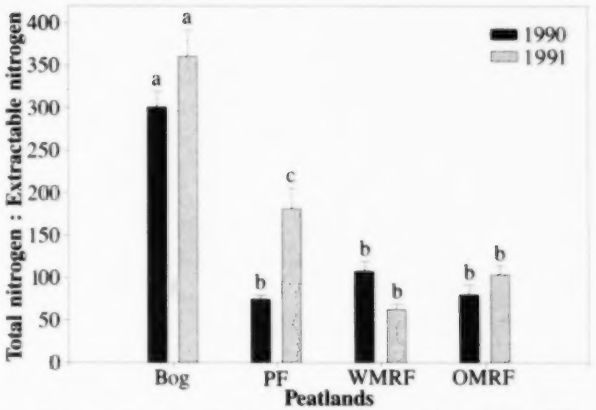

FIGURE 4. Quotients of total nitrogen and extractable nitrogen (+ SE) in peat cores from the bog and three fens in central Alberta, Canada in 1990 and 1991. Site abbreviations as in Figure 1. Different letters indicate significant differences ($P < 0.05$) among peatlands or between years within peatlands. Bog and PF cores, 20 cm long; WMRF and OMRF cores, 15 cm long.

The quotient of TN in vegetation to the soluble N in peat was suggested by Waughman and Bellamy (1980) to be an indication of the degree of N-limitation for peatland vegetation. By using the TN in the surface peat as an indication of the demand for N by the growing bryophytes and the amount of exchangeable NH_4^+-N in the 4-10 cm depth as an indication of the supply available to the plants, we have calculated the ratio of the demand to supply of N for each of the peatlands. Using this approach, the bog has a mean

330:1 requirement for N relative to the available N, while the fens are not as N-limited, ranging from 61 to 180:1 (Figure 4). The net ammonification rate in the four peatlands showed a positive correlation with TN in the "initial" core peat (Figure 3a). The surface of the peat profile has the highest ammonification rate, similar to results by Updegraff *et al.* (1995), and the highest TN concentrations (Tables III and VI) and is equivalent to the litter in a forested system. Pastor *et al.* (1984) in their study of temperate forests did not find a statistical correlation between N mineralization rates and TN concentrations in the forest litter. However, they did find that the TC:TN quotient of litter was highly negatively correlated with the N mineralization rate. Our data also show a highly negative correlation between the TC:TN quotient and net mineralization rate (Figure 3b). The amount of TN in the surface peat (actually the live moss layer) is in excess of the N supplied by mineralization in the top 20 cm of the peat profile on an annual basis. It is likely that additional N is provided by precipitation and by the ground water flow in the moderate-rich fens.

In conclusion, variables that regulate rates of decomposition and mineralization *in situ* could not be separated. Decomposition rates do not appear to regulate mineralization rates and *vice versa*; however, the two processes are tightly linked, supporting hypothesis 3. The lower TC:TN quotients, and hence higher TN tissue concentrations, of the transplanted *C. lasiocarpa* litter, which decomposed rapidly in all four peatlands, suggest that plant chemistry variables influence decomposition and N mineralization rates.

Acknowledgements

We thank S. Campeau, S. Urban, P. Burgess, E. Joyce, G. Hutchinson, L. Halsey, J. Montagnes, and B. Parker for assistance in the field and laboratory. We also thank three anonymous reviewers for their comments on an earlier draft of this manuscript. This work was supported by a National Science and Engineering Research Council (NSERC) grant to S. E. Bayley.

Literature cited

Aerts, R., J. T. A. Verhoeven & D. F. Whigham, 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology, 80: 2170-2181.

Anderson, L. E., 1990. A checklist of *Sphagnum* in North America north of Mexico. The Bryologist, 93: 500-501.

Anderson, L. E., H. A. Crum & W. R. Buck, 1990. List of mosses of North America north of Mexico. The Bryologist, 93: 448-499.

Backéus, I., 1990. Production and depth distribution of fine roots in a boreal open bog. Annales Botanici Fennici, 27: 261-265.

Bartsch, I. & T. R. Moore, 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Canadian Journal of Botany, 63: 1241-1248.

Bellisario, L. M., T. R. Moore & J. L. Bubier, 1998. Net ecosystem CO_2 exchange in a boreal peatland, northern Manitoba. Écoscience, 5: 534-541.

Berg, B. & H. Staaf, 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Pages 163-178 *in* F. E. Clark & T. H. Rosswall (eds.). Nitrogen Cycling in Terrestrial Ecosystems: Processes, Ecosystem Strategies and Management Implications. Ecological Bulletin 33, Swedish Natural Science Research Council, Stockholm.

Bowden, W. B., 1987. The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry, 4: 313-348.

Bridgham, S. A., K. Updegraff & J. Pastor, 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology, 79: 1545-1561.

Bubier, J., A. Costello, T. R. Moore, N. T. Roulet & K. Savage, 1993. Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. Canadian Journal of Botany, 71: 1056-1063.

Chimner, R. A. & D. J. Cooper, 2003. Carbon dynamics of pristine and hydrologically modified fens in the southern Rocky Mountains. Canadian Journal of Botany, 81: 477-491.

Damman, A. W. H., 1988. Regulation of nitrogen removal and retention in *Sphagnum* bogs and other peatlands. Oikos, 51: 291-305.

Environment Canada, 1998. Canadian Climate Normals, 1971-2000. Canadian Climate Program, Ottawa, Ontario. [Online] URL: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html

Farrish, K. W. & D. G. Grigal, 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Science, 145: 353-358.

Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre & A. J. McKerrow, 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecological Monographs, 61: 415-435.

Hobbie, S. E. & L. Gough, 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. Oecologia, 140: 113-124.

Humphrey, W. D. & D. J. Pluth, 1996. Net nitrogen mineralization in natural and drained fen peatlands in Alberta, Canada. Soil Science Society of America Journal, 60: 932-940.

Kennedy, J. B. & A. M. Neville, 1976. Basic Statistical Methods for Engineers and Scientists. 2nd Edition. Harper and Row, New York, New York.

McClaugherty, C. A., J. Pastor, J. D. Aber & J. M. Melillo, 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology, 66: 266-275.

Megraw, S. R. & R. Knowles, 1987. Active methanotrophs suppress nitrification in a humisol. Biology and Fertility of Soils, 4: 205-212.

Mewhort, R. L., 2000. Nitrogen dynamics and ecological characteristics in marshes and fens in boreal Alberta, Canada. M.Sc. thesis, Biological Sciences Department, University of Alberta, Edmonton, Alberta.

Moore, T. R., 1994. Trace gas emissions from Canadian peatlands and the effect on climate change. Wetlands, 14: 223-228.

Moss, E. H., 1994. Flora of Alberta. Revised Edition by J. G. Packer. University of Toronto Press, Toronto, Ontario.

Ohlson, M., 1987. Spatial variation in decomposition rate of *Carex rostrata* leaves on a Swedish mire. Journal of Ecology, 75: 1191-1197.

Parnas, H., 1975. Model for decomposition of organic material by microorganisms. Soil Biology & Biochemistry, 7: 161-169.

Pastor, J., J. D. Aber, C. A. McClaugherty & J. M. Melillo, 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology, 65: 256-268.

Rosswall, T. & U. Granhall, 1980. Nitrogen cycling in a subarctic ombrotrophic mire. Pages 209-234 *in* M. Sonesson (ed.). Ecology of a Subarctic Mire. Ecological Bulletin 30, Swedish Natural Science Research Council, Stockholm.

Roulet, N. T., R. Ash, W. Quinton & T. Moore, 1993. Methane flux from drained northern peatlands: Effect of a persistent water level lowering on flux. Global Biogeochemical Cycles, 7: 749-769.

Saarinen, T., 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. Canadian Journal of Botany, 74: 934-938.

SAS Institute Inc., 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, North Carolina.

Scheffer, R. A., R. S. P. van Logtestijn & J. T. A. Verhoeven, 2001. Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. Oikos, 92: 44-54.

Szumigalski, A. R. & S. E. Bayley, 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. Canadian Journal of Botany, 74: 573-581.

Szumigalski, A. R. & S. E. Bayley, 1997. Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. Ecoscience, 4: 385-393.

Thormann, M. N. & S. E. Bayley, 1997a. Decomposition along a moderate-rich fen–marsh peatland gradient in boreal Alberta, Canada. Wetlands, 17: 123-137.

Thormann, M. N. & S. E. Bayley, 1997b. Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. Plant Ecology, 131: 1-16.

Thormann, M. N. & S. E. Bayley, 1997c. Aboveground net primary production along a bog–fen–marsh gradient in southern boreal Alberta, Canada. Ecoscience, 4: 374-384.

Thormann, M. N., S. E. Bayley & R. S. Currah, 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Canadian Journal of Botany, 79: 9-22.

Thormann, M. N., A. R. Szumigalski & S. E. Bayley, 1999. Aboveground peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in southern boreal Alberta, Canada. Wetlands, 19: 305-317.

Updegraff, K., J. Pastor, S. A. Bridgham & C. A. Johnston, 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications, 5: 151-163.

Urban, N. R. & S. J. Eisenreich, 1988. Nitrogen cycling in a forested Minnesota bog. Canadian Journal of Botany, 66: 435-449.

Verhoeven, J. T. A. & H. H. M. Arts, 1992. *Carex* litter decomposition and nutrient release in mires with different water chemistry. Aquatic Botany, 43: 365-377.

Verhoeven, J. T. A., A. M. Kooijman & G. van Wirdum, 1988. Mineralization of N and P along a trophic gradient in a freshwater mire. Biogeochemistry, 6: 31-43.

Verhoeven, J. T. A., E. Maltby & M. B. Schmitz, 1990. Nitrogen and phosphorus mineralization in fens and bogs. Journal of Ecology, 78: 713-726.

Verhoeven, J. T. A., D. F. Whigham, M. van Kerkhoven, J. O'Neill & E. Maltby, 1994. A comparative study of nutrient-related processes in geographically separated wetlands: Towards a science base for functional assessment procedures. Pages 91-106 *in* W. J. Mitsch (ed.). Global Wetlands Old World and New. Elsevier, New York, New York.

Vitousek, P. M., J. R. Gosz, C. G. Grier, J. M. Melillo & W. A. Reiners, 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs, 52: 155-177.

Vitt, D. H., S. E. Bayley & T.-L. Jin, 1995. Seasonal variation in water chemistry over a bog–rich fen gradient in continental western Canada. Canadian Journal of Fisheries and Aquatic Sciences, 52: 587-606.

Vitt, D. H., L. A. Halsey, M. N. Thormann & T. Martin, 1996. Peatland Inventory of Alberta. Phase I: Overview of Peatland Resources and of the Natural Regions and Subregions of the Province. National Centres of Excellence in Sustainable Forest Management, University of Alberta, Edmonton, Alberta.

Waughman, G. J. & D. J. Bellamy, 1980. Nitrogen fixation and the nitrogen balance in peatland ecosystems. Ecology, 61: 1185-1198.

Williams, R. I. & R. E. Wheatley, 1988. Nitrogen mineralization and water-table height in oligotrophic deep peat. Biology and Fertility of Soils, 6: 141-147.

Yavitt, J. B., R. K. Wieder & G. E. Lang, 1993. CO_2 and CH_4 dynamics of a *Sphagnum*-dominated peatland in West Virginia. Global Biogeochemical Cycles, 7: 259-274.